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The Conditions Favoring Between-Community Raiding in Chimpanzees, Bonobos, and Human Foragers

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Abstract Chimpanzees, bonobos, and human foragers share a fission-fusion social system and a mating system of joint male resource defense polygyny. Within-community skew in male strength varies among and within species. In this study, we extend a mathematical model of within-group male coalition formation among primates to derive the conditions for between-community conflicts in the form of raids. We show that the main factor affecting the presence of successful raiding is the likelihood of major discrepancies in party strength, which are set by party size distributions (and thus community size) and the skew in strength. This study confirms the functional similarities between the raiding of chimpanzees and human foragers, and it supports the "imbalance of power" hypothesis for raiding. However, it also proposes two amendments to this model. First, the absence of raiding in bonobos may be attributable more to potential female involvement in defense against raids, which increases the size of defensive coalitions. Second, the model attributes some of the raiding in humans to major contrasts in instantaneous fighting ability created by surprise raids on unarmed victims; it also draws attention to the distinction between minor raids and major raids that involve multiple bands of the same community.

Key words: Chimpanzees, Human foragers, Bonobos, Warfare, Raids, Intergroup conflict, Mathematical model

Chimpanzees live in fission-fusion communities. All long-term studies report strong territoriality, accompanied by occasional outbreaks of lethal violence aimed at members of other communities (Wilson 2013; Wilson et al. 2014). Chimpanzee parties, consisting mainly of adult males, patrol the boundaries of their territories, especially when fruit is abundant there. These parties may intrude and search for their opponents, and then attack them when the participants perceive a large asymmetry in party size (Wilson et al. 2001). The resulting raids on solitaries or small parties may turn lethal (Mitani et al. 2010; Wilson and Wrangham 2003). This raiding behavior is universal among chimpanzees and not an artifact of provisioning (Wilson 2013; Wilson et al. 2014). Chimpanzees must therefore always live with the threat of lethal attack from their neighbors whenever they come near the boundaries of their territory.

Wrangham and Glowacki (2012) compared these raids with the simple wars found among mobile (nomadic) human foragers and found many functional similarities (see also Diamond 2012; Gat 2006; van der Dennen 1995). Simple war is found in small-scale societies without social stratification. It mainly involves limited surprise raids by parties of ordinary men.

Such comparisons are controversial. It is frequently claimed that in human wars, cultural factors, including ideology, are major determinants (e.g., Robarchek 1989), and that any comparison with nonhuman species is therefore moot. Here, we do not deny the role of ideology or other cultural influences, but we do assume that in simple wars their effect does not systematically skew individual decisions away from their fitness interests (see also Glowacki and Wrangham 2015).

The overall objective of this paper is to examine to what extent the coalitionary violence between communities in chimpanzees (henceforth *chimpanzee raids* for the sake of brevity) and the raiding found among mobile human foragers (henceforth *forager raids*) reflect the same underlying socioecology. If this idea is confirmed, the case for regarding forager raids as a straightforward evolutionary adaptation is strengthened (Gat 2006; Wrangham and Glowacki 2012), even if its expression is no doubt highly conditional.

Our task can be divided into two parts. The first aim of this paper is to identify the key socioecological variables underlying chimpanzee raids, thereby simultaneously explaining the rarity of lethal between-group violence among primates in general. We do this by reviewing the literature on chimpanzee raiding and its predominant functional explanation. We find that human foragers, chimpanzees, and bonobos share the same basic socioecological conditions for raiding, thus providing a platform for more detailed modeling.

The second aim is to develop a simple model for raiding, based on a model for within-group coalitions among primate males (Pandit and van Schaik 2003; van Schaik et al. 2006). If this model replicates the observed patterns in chimpanzees (see Pradhan et al. 2014 for a first attempt), it can then be applied to bonobos and mobile human foragers.

The Socioecology of Chimpanzee Raids

Two major elements of chimpanzee raiding require explanation. First, the major participants are adult males, especially when it comes to escalated attacks. Second, chimpanzee males coordinate their attacks and do not stop when the target attempts to flee; instead they collectively corner, pin down, and maim their victim. Thus, they give the impression of having the intention to kill the opponent, unlike what is seen in virtually all other primate species. These two elements are related.

The sex difference can be linked to asymmetries in the size of potential fitness benefits from attacking other groups. Because female fitness is generally limited by access to resources, the benefits of excluding others from these resources involve rapidly diminishing returns (Trivers 1972). Thus, where females engage in between-group violence, lethal attacks are rare and appear to be the result of attempts to drive the opponent(s) away rather than killing them (Cheney 1987).

Male fitness, in contrast, is generally limited by access to females and is potentially less susceptible to diminishing returns. Indeed, reports of males killing other males are far more common than reports of females killing females (Smuts 1987). However, escalated fights with potentially lethal consequences happen not during between-group encounters but rather most commonly during attempted takeovers of dominance of mixed-sex groups, although there are rare exceptions (e.g., Palombit 1993). This pattern is expected because the mating system of most primate species is female defense polygyny (Emlen and Oring 1977). In this system, escalated attacks during between-group interactions generally do not translate into major fitness benefits because females are unlikely to join the attacker's group. Therefore, because the most likely strategy to increase the number of females to whom access is controlled consists of taking

over another, larger group, escalated violence is seen in that context rather than in the context of between-group conflicts.

In contrast, in resource defense polygyny, males can increase their fitness by increasing the size of their territories. This either increases the area available to the females controlled by the males or attracts additional females. Thus, resource defense polygyny is the most likely context in which male-driven, lethal, between-group aggression should be expected. Because the male bonding in chimpanzees leads them into a coalitionary form of resource defense polygyny, (Goodall 1986; Manson and Wrangham 1991), their mating system is best called *resource defense polygynandry.* This is also found in a few other male-bonded primate species, such as bonobos (Furuichi 2011) and, convergently, atelines (Aureli et al. 2006).

In this system, the role of females could potentially be greater because they too may gain from territory expansion. However, females are forced to share this benefit with others, and the low skew in fitness returns may cause a collective action problem (Willems et al. 2013). Moreover, female participation may also be limited by risk to dependent offspring and the high travel costs involved in patrols and incursions (Amsler 2010). However, females may under some conditions play an important role in defense, when the males under attack are their sons (see below).

In conclusion, the combination of a sex difference in the nature of the factors limiting fitness and a polygynandrous resource defense mating system explains why lethal between-community violence is limited to male-bonded species such as chimpanzees, at least among primates. What this account does not directly explain, however, is why the attacks are so targeted and give the impression of being aimed at killing opponents, rather than merely chasing them away. Nor does it explain why such lethal attacks are not commonly reported for the other primate species with resource defense polygyny, such as bonobos or the atelines.

To close this explanatory gap, Wrangham (1999; Manson and Wrangham 1991) developed the "imbalance of power" hypothesis. Attacks happen when attackers outnumber opponents by at least a factor of 3–4 (see Wilson et al. 2014) because at this margin the attacks are relatively risk-free for the attackers, provided they are well coordinated. Indeed, there are no reports that attackers suffer major injuries. Therefore, these males can afford to go for the kill.

Between-community encounters in bonobos are generally less violent. Bonobos do not engage in patrols and raids and tend to have higher home range overlap (Furuichi 2011; Hohmann and Fruth 2002). The imbalance of power hypothesis suggests that the absence of lethal attacks in bonobos is due to their larger mean party sizes (Furuichi 2009; Wrangham 1986), presumably because of their greater vulnerability to scramble competition (Wrangham 2002). This means that major asymmetries that enable risk-free attacks are rare. However, small parties and solitaries may also be found in bonobos (Boesch and Boesch-Achermann 2000). Thus, we cannot at present exclude two other possibilities. First, bonobo males rarely engage in social hunting (Surbeck and Hohmann 2008). The latter may be a prerequisite for low-risk killing of opponents by providing practice for effective collaboration in high-risk situations. Second, females are dominant to males and have extended periods of sexual activity (Furuichi 2009; Hohmann and Fruth 2002; Surbeck et al. 2011), which is expected to result in generally lower male reproductive skew (although the actual data on this are limited; Gerloff et al. 1999). When skew becomes too low, the males may face a collective action problem and thus refrain from effective between-community contest in the form of raids. The absence of unbiased estimates of each individual's association patterns in chimpanzees and bonobos makes it impossible to resolve this issue for now.

The imbalance of power hypothesis also predicts lethal attacks in the atelines. However, although raids have been observed in spider monkeys (Aureli et al. 2006), lethal attacks have not been described thus far. This absence may be linked to limited observation time (cf. Aureli et al.

2006), to the rarity of instances in which large parties can attack very small parties or solitaries, or to the absence of social hunting.

In sum, then, raiding by male chimpanzees can be understood as a consequence of their living in a male-bonded fission-fusion social system based on a mating system of joint resource defense polygynandry. The fission-fusion element creates potentially large asymmetries in party sizes of neighboring communities. Raiding is perhaps facilitated by social hunting because it reduces the risk to the attackers.

Raiding among Mobile Human Foragers

We are now ready to ask whether mobile human foragers show the same basic socioecology as chimpanzees, and thus whether we can model their between-community raiding in the same way. First, human foragers show evidence for male bonding (Rodseth et al. 1991). Second, human forager communities are usually territorial (Layton et al. 2012). Third, mobile foragers live in fission-fusion societies (Marlowe 2010). In mobile foragers, bands are fluid and often exchange members; thus, the equivalent of the chimpanzee community among foragers is the macro-band or community (Layton et al. 2012). Men tend to hunt together, and women always forage together, and do so in different combinations and party sizes. Thus, the basic assumptions of coalitionary resource defense polgynandry, varying party size and composition, and male cooperation in high-risk conditions made by the imbalance of power model are also met for foragers, although a smaller proportion of the men of a community will be together at any point in time owing to their being doubly fissioned into camps and within camps into hunting parties.

Finally, although there is much confusion over war among pre-Neolithic human foragers (Diamond 2012), and although warfare may have been less frequent among them (Fry 2007), foragers do engage in warfare of some sort (Gat 2006; Keeley 1996; LeBlanc 2003). Forager warfare is generally in the form of raids that are limited in size and involve low risks to the attackers because they involve surprise, are brief, and are not aimed at occupation (Gat 2006; Wrangham and Glowacki 2012). Minor raids, involving just a few men, or sometimes even only a single man, target specific victims and serve as revenge for a particular offense. Although they need not be between communities, they can be. Larger raids, involving dozens of men, are also reported, but battles, in which groups line up and engage in collective violent conflict, are rare and tend not to claim many victims (Gat 2006; van der Dennen 1995).

In conclusion, human foragers experience the same basic socioecological conditions as chimpanzees. If the model reconstructs the known chimpanzee patterns, and is thus likely to capture the essential elements of chimpanzee raiding, we can ask whether a change in the key model parameters toward human forager (or bonobo) values affects the nature of their between-community conflict.

Modeling Approach

We can now develop a model of chimpanzee raiding based on a behavioral-ecology coalitions model in which the main variables are the size of the group or community and the within-group skew in male fighting abilities and in fitness payoffs to the males. The optimality approach assumes that individual males are rational agents, and thus that natural selection has produced optimal decision-making rules that maximize the individual's fitness (Maynard Smith and Parker 1990). We therefore assume that the males participate voluntarily (i.e., without coercion). There is evidence that these assumptions also hold for human foragers (Glowacki and Wrangham 2013).

In this paper, we will consider the fission-fusion community as the group. Whenever all males are not together in a single community, raids by males from other communities are possible. A party is the subset of community members associating at any one time. A raiding coalition can never be larger than a party.

Because raids often happen opportunistically, their exact composition is not predetermined. Any model of raiding must therefore ask which combinations of males produce viable raiding parties. Raids that target the weakest possible parties of the opponent communities are the least risky and thus most likely to be successful. However, there is always some uncertainty as to which enemies a raiding party will encounter.

Although our focus here is on raiding, we must also briefly discuss total war to highlight the main difference with raiding (Diamond 2012; Otterbein 2004). First, in raiding both the raiders and their targets are only a subset of the respective communities, whereas in total war, all of the community's males may choose to join an attacking or defending coalition, and all males are therefore potentially involved. Second, raids are opportunistic, whereas the battles that characterize total war cannot be opportunistic. Third, raids generally end up taking out the weaker enemies, whereas in total war, the optimum strategy is usually to selectively eliminate the dominants (leaders) of the targeted community because winning alliances must defeat the defending alliance, which will inevitably contain its best fighters. Hence, a gradual elimination from the bottom up is not possible in total war, unlike in raiding. Because chimpanzees, bonobos, and human foragers all live in fission-fusion societies, total war is unlikely (Pradhan et al., in prep.), leaving raiding as the only remaining potentially common form of between-community violence.

The immediate outcome of a successful raid may be the death of some members of the targeted community. The indirect outcome is that members of the targeted community reduce the use of certain areas where they are likely to be raided by avoiding them or only going there when they have sizeable parties or in the presence of particularly powerful males. Consequently, the targeted community loses some of its total resource base, which is gradually usurped instead by the attacking community, and often also part of its total fighting ability.

A raid is always profitable to the attackers since it brings some net benefit to all individual participants, although the size of this fitness benefit (payoff) may depend on the male's rank in the dominance hierarchy because the increased access to the newly added zone must be turned into increased fertilizations or increased survival of the offspring he sired. However, a raid can only occur when it is feasible. An opportunistic raid is feasible if the attacking coalition's total fighting ability exceeds that of the defensive coalition (Pandit and van Schaik 2003); the greater the difference in the communities' total fighting abilities, the more likely the raid will be. If the feasibility criterion is not met, the attackers will abort the raid before the actual attack.

Two key variables in the model follow directly from the individual-fitness approach. The first is the skew in strength, or σ, which describes the relationship between individual fighting ability and dominance (Pandit and van Schaik 2003). There are two possible approaches to estimating skew in strength. The first is to make a direct estimate. Although in the absence of pairwise experiments (as in a tournament) this would be extremely difficult (Noë 1994), σ is expected to be higher where dominance hierarchies are linear and steep (as estimated by David scores; Bissonnette et al. 2009) than where they are shallow. Thus, σ for chimpanzees is presumably higher than for bonobos (Stevens et al. 2008). The second approach is based on the assumption that selection produces a strong correlation between a species' values of σ and β (the skew in fitness returns), at least when $\beta <$ ca 0.5 (cf. van Schaik et al. 2006). As argued above, despite the limited data on skew in paternity, the extended sexual activity of bonobo females (leading to thousands of matings per conception) and their dominance over males make it very likely that β is lower for bonobos (Furuichi 2009; Hohmann and Fruth 2002). This would suggest that the values of σ are higher in chimpanzees than in bonobos. This would then provide an approximate estimate of the range (similar to those seen in β; cf. Pradhan et al. 2014).

Estimating σ in human foragers is extremely difficult. By the two measures used for chimpanzees and bonobos, humans should have lower values. Human foragers do not show clear

dominance hierarchies (Boehm 1999), and being largely pair-bonded, mobile foragers also do not show high reproductive skew (Borgerhoff Mulder et al. 2009). However, our ability to kill rivals at a distance using weapons allows us to kill stronger opponents in surprise attacks (Gintis et al. 2015). As a result, a small party of weak fighters can kill a large number of potentially much stronger fighters. Thus, the value of σ in foragers is quite variable but could be extremely high for short, transient moments.

A coalition's strength is simply assumed to be the sum of its members' fighting abilities (Pandit and van Schaik 2003; van Schaik et al. 2006). This assumption was found empirically to work well for small coalitions of males in primates, wolves, and lions (Bissonnette et al. 2009; Liddle et al. 2012). It is probably too conservative in that chimpanzees' total fighting ability increases more than linearly with the number of individuals that join (Wilson et al. 2002), but this merely means that our results are likely to be somewhat conservative.

The second key variable is the size of the community. Usually, and in our previous work, this size, *N*, includes only adult males. Here, we assume that *N* corresponds to the number of able-bodied individuals that may assist in attack and/or defense in a raid. This implies that in other species than chimpanzees, the number *N* may include adult females or even immatures, if they are effective fighters.

In chimpanzees, the number of males per community varies from a few to more than 25 males, but the lowest values in this range may reflect the impact of recent human-induced diseases. We will therefore take the modal range as being 5–10 (Wilson et al. 2014). Bonobo community sizes usually are somewhat smaller, with on average around 4–8 adult males and a comparable number of adult females (Boesch and Boesch-Achermann 2000; Wilson et al. 2014).

As to human foragers, we can recognize a three-tiered social organization, with hunting parties, the camp or band level, and finally the community (Layton et al. 2012). Hunting parties are small, often less than 5, and sometimes men hunt alone. Band sizes are in the order of 25–50 members, and thus have some 5–15 men on average, whereas community sizes on average about 4–5 times larger than those of chimpanzees (Layton et al. 2012), with a total number of adult males in the range of 50 to a few hundred.

When raids target other bands, the band may be the most appropriate unit of analysis, making the average number of men comparable to the number of males in a chimpanzee or bonobo community. Alternatively, if multiple bands come together for raids, we should consider a minimum of 50 men.

The Formal Model

The communities fight over shareable and divisible resources, such as females or food. Community 1 is assumed to have N_1 members whereas community 2 is assumed to have N_2 members. Individual members have a distinct power (dominance) that is determined exclusively by their individual fighting ability within their own community (to avoid confusion, we will refer to rank as a number: so a low number means having high dominance [e.g., the individual ranked number one is the most dominant). Fighting ability reflects the combination of intrinsic strength, access to weapons, skill with weapons, and fight tactics; in human foragers, we expect it to correlate with hunting prowess.

Successful attack is feasible if the attacking coalition's total fighting ability exceeds that of the defending coalition. Here we assume that the community's fighting ability or strength, $S_j(N_j)$, is the simple sum of each individual's fighting abilities (s^i_j; j=1,2 in our case), for those individuals who decided to participate. It is expressed as follows:

$$S_j(N_j) = \sum_{i=1}^{N_j} s^i_j \,.$$

The relationship between a member's rank i in a group j and its fighting ability s_j^i follows a similar relationship as that between rank and payoff (see Pandit and van Schaik 2003). The parameter σ describes this relationship.

In any raiding or intercommunity violence scenario, some cost is inevitably incurred by the participating members in the form of accidental death or injury or loss of time and energy. However, such costs are difficult to quantify in rational fashion and are ignored in this model. This approximation will not fundamentally alter the findings. We will examine the validity of this assertion in the Discussion.

The model thus has six external parameters: N_1, N_2, $S_1(N_1)$, $S_2(N_2)$, σ_1, and σ_2. Since the raids are always profitable for the participants, we formulate the model purely based on feasibility of raiding, i.e., if any particular raid is going to be successful. Coalitions of all possible sizes (party size) in community 1 are systematically compared with coalitions of all possible sizes in community 2, and the model then calculates the proportion of cases in which successful (feasible) raids are possible. The feasibility of a raid is then computed as the combined probability of forming a raiding party of fighting ability f and the probability of not being able to form a defending party of fighting ability f.

$$P_{\sigma_1\sigma_2}(f,N_1,N_2) = p_{\sigma_1}(f,N_1)\times\left[1-q_{\sigma_2}(f,N_2)\right], \qquad (1)$$

where the $p_{\sigma_1}(f,N_1)$ denotes the probability of forming an attacking coalition in community 1 with fight ability of $\geq f$ and $q_{\sigma_2}(f,N_2)$ is the probability of forming a defensive coalition in community 2 with fighting ability $\geq f$. We assume that the formations of an attacking coalition and a defending coalition are statistically independent events, so the total probability can be written as the simple product of the two probabilities.

Computation of $p_{\sigma_1}(f,N_1)$ involves first finding $i_{\sigma_1}^k(f,N_1)$, which is the rank of an individual such that any coalition of k of individuals with rank $i_{\sigma_1}^k(f,N_1)$ or less has fighting ability greater than or equal to f. Using $i_{\sigma_1}^k(f,N_1)$ one can write the number of possible coalitions with k individuals and with a total fighting ability $\geq f$ as

$$\#_{\sigma_1}^k(f,N_1) = 2^{N_1-i_{\sigma_1}^k(f,N_1)}\left\{2^{n_{\sigma_1}^k(f,N_1)} - \sum_{l=0}^{k-1}\begin{pmatrix} n_{\sigma_1}^k(f,N_1) \\ l \end{pmatrix}\right\},$$

where $\begin{pmatrix} \bullet \\ \bullet \end{pmatrix}$ is the binomial coefficient and $n_{\sigma_1}^k(f,N_1) = i_{\sigma_1}^k(f,N_1) - i_{\sigma_1}^{k-1}(f,N_1)$.

The total number of coalitions with fighting ability $\geq f$ is

$$\#_{\sigma_1}(f,N_1) = \sum_{k=1}^{N_1}\#_{\sigma_1}^k(f,N_1),$$

and the probability of having a coalition with fighting ability greater than or equal to f is

$$p_{\sigma_1}(f,N_1) = \frac{\#_{\sigma_1}(f,N_1)}{2^{N_1}}$$

$$\therefore p_{\sigma_1}(f,N_1) = \sum_{k=1}^{N_1}2^{-i_{\sigma_1}^k(f,N_1)}\left\{2^{n_{\sigma_1}^k(f,N_1)} - \sum_{l=0}^{k-1}\begin{pmatrix} n_{\sigma_1}^k(f,N_1) \\ l \end{pmatrix}\right\}$$

We still need to compute $i_{\sigma_1}^{k}\left(f,N_1\right)$ to get the complete expression. Let i_0 be the lowest-ranked individual (i.e., with the highest number ranking) such that a coalition formed by the individuals between i_0 and i_0-k has fighting ability f. Such i_0 can be computed by expressing the fighting ability f as the sum of individual fighting abilities s_1^j between ranks i_0-k and i_0:

$$f=\sum_{i=i_0-k+1}^{i_0}s_1^i=\sum_{i=1}^{i_0}s_1^i-\sum_{i=1}^{i_0-k}s_1^i$$

$$\therefore f=\frac{S_1\left(N_1\right)\left[1-\left(1-\sigma_1\right)^{i_0}\right]}{1-\left(1-\sigma_1\right)^{N_1}}-\frac{S_1\left(N_1\right)\left[1-\left(1-\sigma_1\right)^{i_0-k}\right]}{1-\left(1-\sigma_1\right)^{N_1}}$$

$$\therefore i_0=\frac{\ln\left(\frac{f}{S_1\left(N_1\right)}\right)+\ln\left[1-\left(1-\sigma_1\right)^{N_1}\right]-\ln\left[\left(1-\sigma_1\right)^{-k}-1\right]}{\ln\left(1-\sigma_1\right)}$$

Thus we write

$$i_{\sigma_1}^{k}\left(f,N_1\right)=\begin{cases}0 & k-1\geq i_0\\ i_0 & k-1<i_0\leq N_1\\ N_1 & N_1<i_0\end{cases}$$

We assume that, irrespective of the target of the raid, the payoff is extracted from the lowest-ranked members in the community. However, it is possible that the lowest-ranking individuals in community 2 may form a coalition and prevent this from happening. For a community with monotonically decreasing fighting ability as a function of rank, there is a particular rank, we will call pivot point (j_p), for which the coalition of males with rank numbers greater than the pivot may overpower the coalition of the dominants. Under such a condition, the top-dominant individuals will also be forced to join the defending coalitions, provided they can afford being in association. Hence, if the attackers' fighting ability f is greater than FA_p, the fighting ability of the coalition of individuals below the pivot (with higher rank numbers and therefore lower-ranked), then the entire community has an incentive to join the defensive coalition in order to prevent a leveling coalition against the dominants (Pandit and van Schaik 2003). First we will compute j_p as the point where the combined fighting ability of individuals above the pivot point is less than or equal to that of the rest of the community.

$$\sum_{i=j_p}^{N_2}s_2^i\leq\sum_{i=1}^{j_p-1}s_2^i$$

$$\therefore S_2\left(N_2\right)\leq 2\sum_{i=1}^{j_p-1}s_2^i$$

$$\therefore \frac{1}{2}\leq\frac{1-\left(1-\sigma_2\right)^{j_p-1}}{1-\left(1-\sigma_2\right)^{N_2}}$$

$$\therefore j_p=ceil\left\{\frac{\ln\left[\frac{1}{2}+\frac{1}{2}\left(1-\sigma_2\right)^{N_2}\right]}{\ln\left(1-\sigma_2\right)}+1\right\}$$

The pivot point j_p is then used to find FA_p, the combined fighting ability of individuals below it.

$$FA_p = \sum_{i=j_p}^{N_2} s_2^i = S_2(N_2) - \sum_{i=1}^{j_p-1} s_2^i$$

$$\therefore FA_p = S_2(N_2)\left\{\frac{(1-\sigma_2)^{j_p-1} - (1-\sigma_2)^{N_2}}{1-(1-\sigma_2)^{N_2}}\right\}$$

Following arguments similar to the attacking side, we write probability of formation of defensive coalition

$$q_{\sigma_2}(f,N') = \sum_{k=1}^{N'} 2^{-i_{\sigma_2}^{'k}(f,N')}\left\{2^{n_{\sigma_2}^{'k}(f,N')} - \sum_{l=0}^{k-1}\begin{pmatrix} n_{\sigma_2}^{'k}(f,N') \\ l \end{pmatrix}\right\},$$

where

$$N' = \begin{cases} N_2 - j_p + 1 & if \quad f < FA_p \\ N_2 & if \quad f \geq FA_p \end{cases},$$

$$n_{\sigma_2}^{'k}(f,N') = i_{\sigma_2}^{'k}(f,N') - i_{\sigma_2}^{'k-1}(f,N'),$$

$$\therefore i_0' = \frac{\ln\left(\frac{f}{S_2(N_2)}\right) + \ln\left[1-(1-\sigma_2)^{N'}\right] - \ln\left[(1-\sigma_2)^{-k}-1\right]}{\ln(1-\sigma_2)},$$

and

$$i_{\sigma_2}^{'k}(f,N') = \begin{cases} 0 & k-1 \geq i_0' \\ i_0' & k-1 < i_0' \leq N' \\ N' & N' < i_0' \end{cases}.$$

Finally we plot the probability of a successful raid (Eqn 1) as a function of the size of the community and the within-community skew in fighting ability (Figure 1). To keep the analysis simple, throughout this paper we assume that the attacking and defending communities are identical, i.e., (N=)N_1=N_2, ($S(N)$=)$S_1(N_1)$=$S_2(N_2)$, and (σ=)σ$_1$=σ$_2$. We also assume that the total fighting ability is a simple linear function of, i.e., $S(N)$=S×N.

Results

General

Figure 1 shows the probability of successful raids by community 1 on community 2, for combinations of within-community skew in fighting ability (σ) and the fighting ability (f) of the raiding community for communities of various sizes (N). There are three main general findings. First, raids are generally expected to be more common in communities with fewer adult males (Figure 1a). This result arises because in such communities, situations in which solitary males encounter larger parties will be relatively more common. Second, small raids, involving 5 males or less, should generally be less common as the number of males per community increases because in larger communities most parties will be larger and major discrepancies are less likely.

Third, raids should become more likely as σ increases: at higher σ, the variability in total fighting ability of parties of the two communities increases, and thus the likelihood of major discrepancies in total fighting ability increases as well.

In addition, in Figures 1b and 1c very large raids are unlikely to succeed because they will elicit large defending coalitions containing the whole community as a result of the threat of within-community leveling coalitions (see discussion on pivot point in previous section). Thus, very large raids are unlikely.

Comparing Species

Let us now interpret the model's outcomes for each of the three species considered here. For chimpanzees, the model correctly predicted that small raids should be common. Large raids, which can only be mounted by large communities, should be rare. In practice, the unusually large community of Ngogo in Uganda (Mitani et al. 2010) may be the most likely to raid among all (Wilson et al. 2014). The most likely explanation is that the model assumes that neighboring communities are of the same size. Where a much larger community neighbors a much smaller one, and if this difference is expressed in comparable asymmetries in mean party size, it will probably engage in frequent raids.

The model also predicted some raiding in bonobos, although such events are not known in the real world. Below, we will discuss this interesting discrepancy in detail.

Turning now to mobile foragers, we should expect raids at two levels: opportunistically by hunting parties or members of the same band joining together, or by members of multiple bands of the same community, which requires deliberate recruitment. The first level corresponds to Figure 1a and 1b. Such minor raids should be common and include the targeted revenge raids described in the ethnographic literature (e.g., Gat 2006). Raids involving multiple bands correspond to the bottom panel (Figure 1c).

Given the presence of weapons (see above), humans can have high effective σ, perhaps even exceeding the upper level of chimpanzees. Thus, mid-sized and even larger raids should also be expected when the surprise element works (obviously, then raids are no longer opportunistic). This also corresponds to the literature (Gat 2006; van der Dennen 1995).

Discussion

We established fundamental similarities in the socioecology of chimpanzees and bonobos on the one hand and human foragers on the other hand. Both are based on coalitionary resource defense polygyny, in which raids are the only adaptive means to defend and expand the joint territory. This similarity allowed us to develop a model for male-bonded raiding and apply it to all three species.

Before we review the results of each species in more detail, we must examine some critical assumptions. First, our approach ignores costs because they cannot be estimated. However, the absence of injuries in the documented chimpanzee raids (Wilson et al. 2014) and their low incidence in forager raids (Gat 2006) suggests that the main costs are energetic (cf. Amsler 2010). This is probably because the risk of injury or death, and thus cost, is inversely proportional to the difference in fighting abilities of the two sides. Thus, we envision that the introduction of costs should result in the blurring of the raid/no raid boundary but essentially leave the predictions unchanged.

The second assumption is that the males in a community are not closely related. If they are, this may have two consequences. First, within-community reproductive skew becomes important and total war becomes more likely. The other consequence is potentially more far-reaching. The model assumes that the strongest males in community 2 do not come to the aid of the peripheral lower-rankers that are picked off by the raids. If they all were highly related, these

males might come to their aid by increasingly associating with them. This will either lead to all-out war or (more likely) the cessation of raiding.

It is therefore important to examine the role of relatedness in practice. Field data on chimpanzees have shown that the males in alliances are not more closely related than the community's (and presumably population's) average (Langergraber et al. 2007). The same may also be true for human foragers (cf. Macfarlan et al. 2014), perhaps as a result of the relatively low reproductive skew. This is consistent with the low genetic differentiation between neighboring communities (Langergraber et al. 2011). Thus, the assumption of low relatedness among males is probably justified.

Chimpanzees and Bonobos

The model predicted that chimpanzees should frequently have small raids (Fig. 1a) and suggested that very large communities could also raid (Fig. 1b). This is consistent with the real-world data. However, in the model the neighboring communities are of the same size. Large discrepancies in the sizes of neighboring communities, if accompanied by concomitant discrepancies in party size, may also produce raiding by the larger community.

Finer-grained predictions are also possible. Raids are most likely when larger, stronger parties meet smaller, weaker ones. The likelihood of this happening is related to the number of males in a community and σ, the skew in male fighting ability. However, the model estimates the likelihood of raiding by systematically comparing all possible combinations of party strengths on the two sides, where each party's strength is the sum of the number of males weighted by their strength. If solitaries or small parties are rare because the ecology allows individuals to avoid this situation, raids should be less common (Wrangham 1999). This variation in the presence of small parties or solitaries may explain the variation in raiding among chimpanzee populations. Estimates of raiding are clearly higher in East African chimpanzee populations than in the West African site of Taï Forest (Boesch et al. 2008; Wilson et al. 2014). The Taï chimpanzees are more systematically gregarious than East African ones (Lehmann and Boesch 2004).

The model did not correctly predict the bonobo pattern. One possible explanation is that in bonobos very small parties are rare (Wrangham 1999). However, some authors doubt that this is the case (Boesch and Boesch-Achermann 2000). We therefore examine another factor as well: the role of females. In bonobos, females may have to be added to party size. Although females do not participate in attacks, they should participate in defensive actions whenever they can stand their ground against males. This has been amply documented in bonobos (Surbeck et al. 2011; Vervaecke et al. 2000). As a result, defensive parties will generally be larger, given that male bonobos are often in mixed-sex parties (Furuichi 2011; Hohmann and Fruth 2002). Obviously, if only mothers participate in defense (cf. Furuichi 2011), the effective increase in defensive party size may be modest, but an attacking party would not be able to predict which of the associated females will be effective defenders. Thus, the presence of females as defenders should make raiding less likely (move from Figure 1a to 1b at the same σ).

This conclusion must remain speculative at this point. First, unbiased estimates of party-size distributions might reveal a substantial number of solitaries or small parties in bonobos. Second, it still remains possible that bonobos do not raid because they lack the ability to coordinate effective joint attacks in high-risk situations. Bonobos seldom (if ever) engage in high-risk social hunting. In chimpanzees, it is possible that social hunting was a precondition for the evolution of effective raiding, although the finding that hunting and raiding tendencies may be regulated independently in chimpanzees (Gilby et al. 2013) argues against this idea. If lethal raids will be described for atelines, this possibility can be definitively rejected.

In conclusion, if the model is adjusted for patterns in party size and female fighting ability, we obtain the correct predictions. Thus, in effect, imbalance of power explains the

variation among chimpanzees and bonobos, as predicted by Wrangham (1999) and Wilson et al. (2014), but perhaps largely because of the effective defense by females.

Finally, it is interesting to ask whether raids can lead to the extinction of communities. The model does not differentiate between removing the lower-ranked males of the neighboring community by chasing them away or by killing them. However, killing may be a far more effective way of eliminating males from the rival community because merely having to flee once in a while may be an acceptable cost and therefore does not result in permanent abandonment of the contested area. Thus, in principle we should expect communities with large male parties to drive neighbors with smaller male party sizes to extinction. To date, two community extinctions have indeed been recorded, one each at Gombe and Mahale, both in East Africa (although in the latter case no actual killings were observed).

Under the model, we expect that communities that lost fighters to raids will at one point respond by forming coalitions involving all fighters (because of the upward shift of the pivot point j_p). As a result, raiding by the original attackers should decline, unless there is a major discrepancy in total community sizes. Thus, the model may suggest an alternative explanation for the observed extinctions of whole communities. They may be unusual outcomes fueled by the provisioning of the attacking communities. Male decisions to go on a raid are directly affected by their body condition (and thus the immediate need to feed) and the size of the male party (and thus local fruit abundance). In natural conditions, male parties are larger when fruit is abundant (Watts and Mitani 2002). In provisioned communities, larger male parties may therefore be more common, whereas this is not the case in similar-sized neighboring communities, and thus raiding may become more severe than otherwise. If such larger raids are both systematic and one-sided, one community may eventually exterminate the other. Indeed, in both recorded cases, the putative attacking community was provisioned (Goodall 1986; Nishida et al. 1985; Wilson et al. 2014). This speculation can be tested by comparing male party sizes and patrolling frequencies during the period of provisioning and after provisioning was ended, but we are not aware of published data allowing this test. Thus, it remains unclear how often communities will go extinct because of persistent one-sided raiding. What is clear, however, is that chimpanzee communities are always in a state of latent war, and that small parties near the boundary are always at risk of being attacked.

Forager Raiding and Warfare

The model results show that minor raids by a few men should be common. Figure 1b also indicates that medium-sized raids, comprising most men in a band, may also occur between bands of neighboring communities, albeit rarely. Larger raids (Figure 1c) may not be as easy to organize because most bands range independently and rarely come together.

Raids in human foragers are like those in chimpanzees in that they set out to kill the enemy and can be called off at any moment during the process when risk is not as low as anticipated. However, they differ from those in chimpanzees in that men can kill at a distance (Gintis et al. 2015). As a result, low-risk raids may require a less dramatic asymmetry in party strength, provided that the element of surprise is great, because it produces large instantaneous discrepancies in the fighting ability of the attacking and the defending coalitions. Thus, the model systematically underestimates the incidence of raids. In effect, we should examine Figure 1 for higher values of σ to obtain the correct prediction.

In sum, the availability of long-distance weapons may have greatly increased the incidence of raiding in human foragers. The latter may thus have begun to rise after the invention of these weapons (throwing spears), some 500,000 years ago (Wilkins et al. 2012), and later intensified after the invention of bows and arrows. Likewise, the coordination of mid-sized or

larger raids, which cannot rely on men simply coming together for a hunt, may also have required language, which arose around the same time or earlier (Dediu and Levinson 2013).

Implications for Modern Wars

The face of human war has changed dramatically over the past 10,000 years (Otterbein 2004), leading many (e.g., Thorpe 2003) to argue that the raiding of foragers is irrelevant to the understanding of modern warfare. However, a better understanding of raiding warfare may confirm its foundational role in the cultural evolution of human war.

Raiding psychology has two elements: an offensive and a defensive one. Chimpanzees engage in raids whenever they can gain an easy victory. They are therefore in a permanent state of latent war. This leads to a psychology of constant fear of being killed by surprise attacks, as well as a tendency toward opportunistic attacks on unthreatening neighboring communities if risk is perceived to be low. These two tendencies can feed on each other because conducting successful preemptive strikes when the conditions present themselves may prevent future attacks.

The fundamental similarity between raiding in chimpanzees and human foragers confirmed in this study suggests that the same basic decision rules also govern the raids in mobile human foragers. However, unlike chimpanzees, humans are able to gain benefits from social interactions with neighbors through trade or alliance formation, producing peaceful relations (Wilson 2013). Moreover, in large-scale societies, in addition to stalemate, elimination, or peace, there also is the option to merge social units to form new ones.

These new options may produce more benign attitudes toward neighboring societies. However, they are almost certainly based on cognitive rather than emotional processes, which they complemented but did not replace. Moreover, trade and exchange do not guarantee that preventive surprise attacks will not happen; thus, suspicion and its consequence, preemptive attacks, need not disappear, nor will its emotional basis. We should therefore expect that the basic emotions governing attitudes toward war have remained stable through evolutionary time, but have been tempered by cognitive deliberations.

This combination of emotional and cognitive elements should make us vulnerable to suboptimal decisions in modern, large-scale societies when they yield different courses of actions. Perhaps more importantly, it enables elites or ideologues to manipulate the emotions of others. Indeed, Wrangham and Glowacki (2012) have suggested that the high mortality risks faced by attacking groups in modern war may be the product of ideology, imposed on warriors (but see Rusch 2014).

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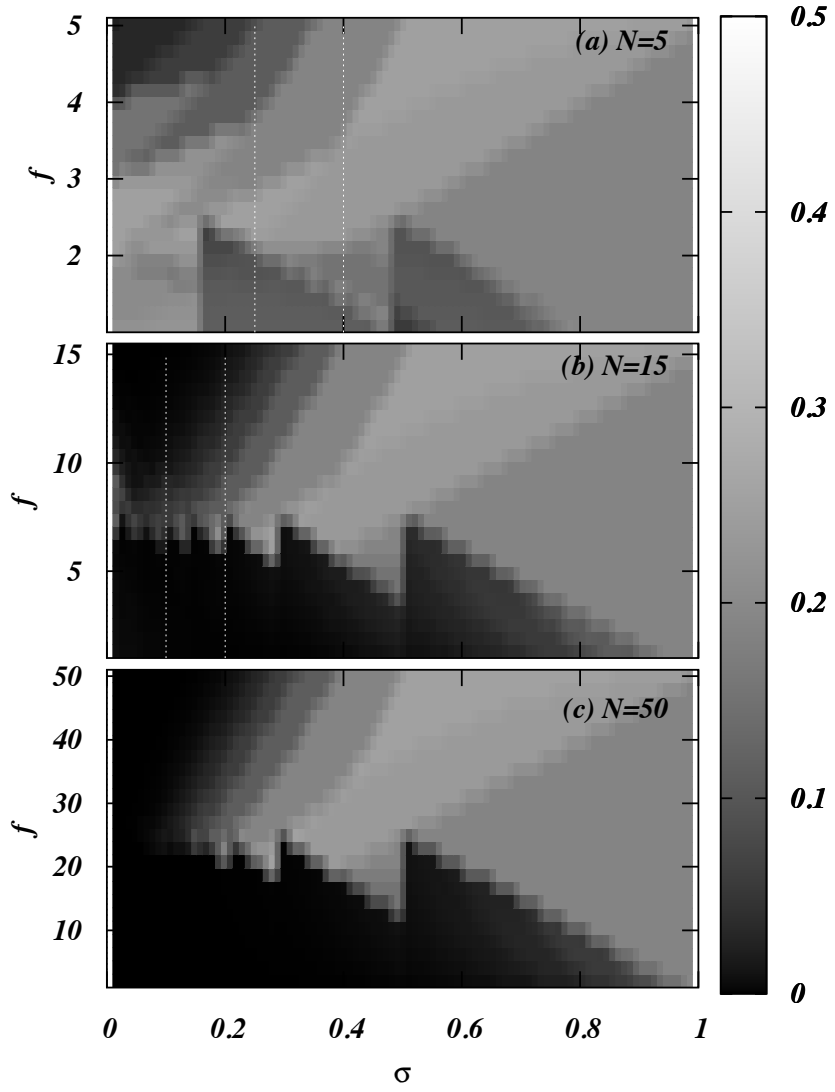
Fig. 1 The probability of successful raids of size f, as a function of the strength of the within-community skew in fighting ability, for three sizes of communities (where N is the number of fighters, usually males). **a** mostly refers to chimpanzees; **b** mostly to bonobos because adult females can be effective defenders, thus raising effective N. The thin vertical lines mark the approximate lower and upper bounds of the skew found in chimpanzees (a) and bonobos (b). When applied to foragers, **a** and **b** also give the results for small and mid-sized band-level raids, whereas **c** gives the results for raids involving multiple bands.


(a) N=5
(b) N=15
(c) N=50
f
5
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3
2
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